

Visceral Helminths from an Expanding Insular Population of the Long-nosed Armadillo (*Dasypus novemcinctus*)

ANDREW A. RADOMSKI,¹ DAVID A. OSBORN,¹ DANNY B. PENCE,^{2,4}
MARTIN I. NELSON,³ AND ROBERT J. WARREN³

¹ Department of Range and Wildlife Management, Texas Tech University, Lubbock, Texas 79409,

² Department of Pathology, Texas Tech University Health Sciences Center, Lubbock, Texas 79430, and

³ School of Forest Resources, The University of Georgia, Athens, Georgia 30602

ABSTRACT: Long-nosed armadillos (*Dasypus novemcinctus*) ($N = 117$) from Cumberland Island, Georgia were infected with encysted cystacanths of *Macracanthorhynchus ingens* and *Centrorhynchus* sp. and larvae of *Physaloptera* sp. Ninety-five, 56, and <3% of the hosts had 1, 2, and 3 species of helminths, respectively. The frequency distribution pattern of each helminth species was aggregated; overdispersion was homogeneous across host sex and season variables. Abundances of all helminth species collectively, and *Physaloptera* sp. individually, were significantly greater in the warm versus cool seasons. As a corollary to Brown's (1984) theory, we propose that a host population at the periphery of its geographic range may have fewer species and lower abundances of helminths and/or lack a defined helminth community when compared to a conspecific population at the host's epicenter of origin. This may partially explain why a community of species of adult helminths has not developed in the recently colonized population of armadillos on Cumberland Island. Other reasons for this vacant niche may include (1) the unique physiology of armadillos may preclude them as a suitable definitive host for helminths already on the island; (2) there are no other related hosts on the island with a community of helminth species that could infect the armadillo; and (3) the founders of this armadillo population were not infected prior to colonizing the island.

KEY WORDS: Brown's theory, *Dasypus novemcinctus*, geographic barrier, helminth community ecology, helminth survey, host colonization, insular host population, long-nosed armadillo, range periphery, physiological barrier, unsuitable host, vacant niche.

The range of the long-nosed armadillo (*Dasypus novemcinctus* Linnaeus) extends from the southern United States through Mexico and Central America into South America as far south as Uruguay (McBee and Baker, 1982). Armadillos were first reported in the United States in 1854 from southern Texas (Bailey, 1905). Subsequently, they have expanded their range northward and eastward from the Texas population and northward from expanding populations introduced in Florida in the early 1920's (Cleveland, 1970). Active invasion at a rate of 4-10 km/yr has extended the present distribution of armadillos from central Kansas eastward to South Carolina (Humphrey, 1974; Mayer, 1989).

Invasion of a species into a new locality may be more successful if the colonizing species is free from specific pathogenic parasites infecting it in the original habitat. Possible examples of this in species that have invaded North America include house sparrows (*Passer domesticus*) and starlings (*Sturnus vulgaris*), both of which have fewer species of parasites than their European counterparts (Dobson and May, 1984). Although

the long-nosed armadillo recently has colonized a large area in the southeastern United States, the few helminth surveys indicate that the invading population has only a fraction of the helminth species (Taber, 1945; Chandler, 1946, 1954) reported in this host from its native range in Central and South America.

Although islands are favored study-sites of ecologists, there are few studies (Kisielewska, 1970) on the acquisition of helminths by invading insular vertebrate hosts. Specimens collected in conjunction with other studies on the long-nosed armadillo population of Cumberland Island, a barrier island on the coast of Georgia, provided a unique opportunity to determine the recruitment and establishment of helminths in a recently colonized insular host population. Our objectives were to examine the structure (composition and abundances of species) and pattern (frequency distribution, species richness, effects of extrinsic and intrinsic variables) of the assemblage of species of helminths that have been acquired by this armadillo population since it was introduced to the island; specifically, if a community of helminth species has become established within this host.

⁴ To whom reprint requests should be addressed.

Materials and Methods

Study area

The 25-km-long \times 1–9-km-wide, or 9,400-ha (including salt marshes) Cumberland Island, is the most southern and largest of Georgia's barrier islands. Located in Camden County, Georgia (30°48'N, 81°26'W), Cumberland Island is separated by a linear distance of about 2 km from the mainland by the Cumberland River and Cumberland Sound (Hillestad et al., 1975). In 1972, Cumberland Island was designated a National Seashore and incorporated into the National Park System; prior to this, it was privately owned. The island's natural history and ecology have been described in detail by Hillestad et al. (1975) and summarized by Pence et al. (1988b).

Armادillos were first reported on Cumberland Island in 1973 (Hillestad et al., 1975); they are now abundant in most vegetated upland habitats. This insular population of armadillos became established either through human introduction or by natural invasion from the nearby mainland where armadillos were present at least since 1954 (Humphrey, 1974). Other introductions to the island during the past 10–20 yr include feral populations of swine, horses, and cattle (Hillestad et al., 1975).

Collection of data

In conjunction with other physiological and ecological studies by the junior authors (R.J.W. and M.N.), 117 armadillos (67 males and 50 females; 110 adults, 7 juveniles <1 yr old) were collected from Cumberland Island by shooting during 4–7-day collection periods in late March ($N = 28$), mid-June ($N = 31$), late August ($N = 29$) and mid-December ($N = 29$) 1987. The June and August collections were the warm season sample, while the March and December collections were the cool season sample. About 80% of the armadillos were collected in oak-palmetto and oak-pine habitats. These habitats comprise 61% of the island's forested area (Hillestad et al., 1975). Carcasses were weighed, sexed, and immediately frozen (Pence et al., 1988a). Age was based on the assumption that individuals weighing <3.0 kg were <1 yr old (McNab, 1980). All internal organs were examined; helminths were removed, identified, and quantified. Thin blood smears, prepared in duplicate immediately following death of the armadillos, were stained 10 min with phosphate-buffered Giemsa (pH 7.2) after fixation in 100% methanol for 1 min; they were examined microscopically for filariid nematodes. Necropsy techniques followed the procedures outlined by Wobeser and Spraker (1980), except that visual examination of organ contents was supplemented by repeated washings and sedimentation in conical glasses followed by examination of the sediment with a dissecting microscope. Contents of the stomach were removed for studies on food habits and nutritional ecology.

Nematodes were fixed briefly in glacial acetic acid, stored in a mixture of 70% ethyl alcohol with 8% glycerine, and examined in glycerine wet mounts. Acanthocephalans were fixed and stored in alcohol-formalin-acetic acid (AFA) solution, stained with Semichon's acetocarmine, cleared in oil of wintergreen, and mounted in Canada balsam. Representative specimens of the

helminth species collected in this study are deposited in the U.S. National Parasite Collection (Beltsville, Maryland 20705, USA; accession numbers 80826–80828).

Analysis of data

Overdispersion was indicated when the variance was significantly larger than the mean (by chi-square analysis) in the frequency distribution of the respective helminth species, and was defined by the negative binomial parameter k (Bliss and Fisher, 1953). Homogeneity in the values of k generated from the helminth species' frequency distributions across host and seasonal variables were calculated by the method outlined in Wallace and Pence (1986) as modified from Bliss and Fisher (1953).

The main and interactive effects of 2 independent host variables (sex and season) on the numbers of individuals (abundances) of each species of helminth were examined with a factorial ANOVA, and for all species collectively with a subsequent MANOVA (PROC GLM, SAS; SAS Institute, Inc., 1985). Potential factors influencing abundances of these helminths were sex, season, and sex-season. Age could not be considered as a variable in the analysis because the sample size of the cohort of animals <1 yr old collected during the warm season was too small.

Definitions

The terms prevalence, intensity, mean intensity, and abundance follow the definitions of Margolis et al. (1982). Overdispersion is defined by Bliss and Fisher (1953); the term is used herein to describe aggregated helminth frequency distributions as outlined by Wallace and Pence (1986). Helminth community herein refers to an assemblage of helminth species occupying a certain site (habitat) within the host.

Results

The helminth fauna

Two larval acanthocephalans (*Macracanthorhynchus ingens* (Linstow, 1879) Meyer, 1933 and *Centrorhynchus* sp.) encysted as cystacanths on the serosal surface of the gastrointestinal tract and in the mesenteries, and a larval nematode (*Physaloptera* sp.) from the lumen of the small and large intestines, were found. This is the first report of *Centrorhynchus* sp. from the long-nosed armadillo. Table 1 lists the prevalences, intensities, and abundances of these helminth species. Armadillos were infected with none to 3 ($\bar{x} = 2.2$) species of helminths. The number of armadillos infected with 1, 2, and 3 species of helminths were 111 of 117 (95%), 66 of 117 (56%), and 3 of 117 (<3%), respectively. There were 6,363 helminths collected from the armadillos; abundances ranged from 0 to 481 ($\bar{x} = 14.6 \pm 5.0$). Microfilariae were not observed in the blood smears.

Table 1. Visceral helminths of an insular population of long-nosed armadillos from Cumberland Island, Georgia.

Species of helminths	Prevalence					Total
	Number infected/ Number examined	%	Intensity	Abundance		
			$\bar{x} \pm SE^*$	Range	$\bar{x} \pm SE^*$	
<i>Macracanthorhynchus ingens</i>	11/117	95	47.6 \pm 7.3	0–432	41.1 \pm 6.4	4,628
<i>Centrorhynchus</i> sp.	5/117	4	2.2 \pm 0.7	0–5	0.1 \pm 0.3	11
<i>Physaloptera</i> sp.	75/117	65	22.5 \pm 7.6	0–481	14.6 \pm 5.0	1,724

* Mean \pm standard error.

Helminth dispersion patterns

As characteristic of an overdispersed distribution (Bliss and Fisher, 1953), the variance was significantly larger than the mean for the frequency distributions of helminth individuals in each of the 3 species (Table 2). As indicated by Bliss and Fisher (1953) and outlined by Wallace and Pence (1986), the low values (<1.0) for the negative binomial parameter k in each of these species, indicated aggregation within the host population and within each of the 2 host subpopulations delineated by host sex and season variables. However, values of k were not significantly different across these host subpopulations when compared to the average (expected) value for the entire dataset (Table 2); thus, the degree of overdispersion was homogeneous across these subgroups of the host population.

Effects of intrinsic and extrinsic variables

The main effect of season accounted for significant differences in the numbers of individuals of all helminth species collectively (MANOVA) and individually (factorial ANOVA) for a single species (Table 3). Respectively, this resulted from the greater collective abundance of both *M. in-*

gens and *Physaloptera* sp. and the significantly greater abundance of *Physaloptera* sp. in the warm versus cool seasons. The number of helminth individuals collected during the warm and cool seasons were 4,148 and 2,364, respectively. Mean abundances were 48.2 ± 9.5 , 0.1 ± 0.1 , and 20.9 ± 8.6 versus 33.7 ± 8.8 , 0.1 ± 0.1 , and 8.0 ± 4.8 for *M. ingens*, *Centrorhynchus* sp., and *Physaloptera* sp., respectively.

The number of individuals of *M. ingens* varied across host sexes. There were significantly greater abundances of *M. ingens* in females (61.6 ± 12.7) than males (25.9 ± 5.6).

Discussion

All the helminths in armadillos from Cumberland Island were larvae, most of which were encysted and frequently were dead and calcified. The adults of *M. ingens* occur in carnivores, especially raccoons (*Procyon lotor*) (Petrochenko, 1958). The definitive hosts of *Centrorhynchus* spp. are terrestrial birds, especially raptors (Petrochenko, 1958). Adult *Physaloptera* spp. occur in many species of wild and domestic mammals (Levine, 1968). The frequency distributions and abundances of these larval species tend to follow

Table 2. Values of k as an inverse measure of overdispersion for 3 species of helminths across 4 major category variables delineated by host sex and season from the 117 sample dataset of the long-nosed armadillo from Cumberland Island, Georgia.

Species of helminth	Total (117)	Season				Heterogeneity	
		Cool		Warm		Total χ^2	P
		Male (31)	Female (26)	Male (36)	Female (24)		
<i>Macracanthorhynchus</i> sp.	0.36*	0.47*	0.36*	0.35*	0.35*	0.05	>0.05
<i>Centrorhynchus</i> sp.	0.47	0.16	—	—	0.10	0.51	>0.05
<i>Physaloptera</i> sp.	0.07*	0.06*	0.26*	0.12*	0.12*	0.55	>0.05

* Variance significantly larger than mean as determined by chi-square analysis of the frequency distribution.

Table 3. *F* values generated by MANOVA and factorial ANOVA for main and interactive effects of host sex and season factors across the 117 sample dataset of rank abundances for 3 species of helminths in the long-nosed armadillo from Cumberland Island, Georgia.

	Sex	Season	Sex × Season
MANOVA			
Total helminth species	1.68	3.59*	0.93
Factorial ANOVA			
<i>Macracanthorhynchus ingens</i>	4.75*	3.71*	0.02
<i>Centrorhynchus</i> sp.	0.01	0.04	2.57
<i>Physaloptera</i> sp.	0.41	6.73*	0.17

* Significant at $P < 0.05$.

similar patterns to those described for populations of adult helminths in other host species (i.e., Wallace and Pence, 1986). Obviously, the armadillo is a paratenic host for these helminths, which probably were acquired incidentally through ingestion of arthropod intermediate hosts and after immigration to the island. Because just 3 species of larval helminths were found, and only 2 of these were encysted at the same site, the armadillo population on Cumberland Island has not yet acquired a defined helminth community.

The theory of Brown (1984), which interprets the relationship between abundance and distribution of animal species, was extrapolated to helminth communities by Fedynich et al. (1986) in order to help explain the disparity of helminth species in a beaver (*Castor canadensis*) population at the southern periphery of its native range. While the stable high population densities at the host's epicenter of origin tend to support larger numbers of more numerous species of helminths (a well-developed helminth community), the unstable lower population densities of a host species at the periphery of its range may support fewer numbers and species of helminths (diminished or no helminth community). This may partially explain the lack of species diversity and low numbers of helminths in the long-nosed armadillo from the United States, and, specifically, the absence of a helminth community in the armadillo population from Cumberland Island, which is at the extreme northeastern periphery of its range.

Vertebrate hosts at the extreme periphery of

their range may outdistance many of their helminth parasites; however, some hosts such as raccoons in Saskatchewan (Hoberg and McGee, 1982) and coyotes (*Canis latrans*) in Tennessee (Pence, 1989) can acquire new species from taxonomically related host species in the new locality as replacements for those lost from their original helminth community. Because adult helminths were not found, it appears that the armadillo is not a suitable definitive host for any helminth species already established on Cumberland Island. The long-nosed armadillo is the only extant representative of the mammalian order Xenarthra (Edentata) in North America (Cleveland, 1970). Lack of closely related host species with established helminth communities greatly reduces the chances for acquisition of adult helminths by an invading species (Pence, 1989). This we define as (1) the unsuitable host hypothesis.

There are at least 52 species of adult helminths in the long-nosed armadillo and related species from Central and South America (Chandler, 1946). Although only 3 species of adult helminths were found in this host from Texas, there were several encysted larval acanthocephalan and nematode species (Chandler, 1946). Unfortunately, we could not sample armadillos from the mainland adjacent to Cumberland Island. However, if a helminth community or even individual species of adult helminths did occur in armadillos on the mainland, then those hosts that emigrated to the island must not have been infected with sufficient numbers of helminths to establish and/or maintain a helminth community. This we propose as (2) the geographic barrier hypothesis.

A final tentative explanation for the absence of a helminth community in armadillos on Cumberland Island is that the unique physiological features of the Dasypodidae may prevent establishment, growth, and/or reproduction of certain common helminth species that have little host specificity and are otherwise widely distributed across many different mammalian host taxa. These unique features include low body temperatures (31°–38°C) and a physiology similar to poikilotherms (Chandler, 1954) in which thermoregulatory mechanisms include shivering, changing posture, and probably vasoconstriction (Galbreath, 1982). This we term (3) the physiological barrier hypothesis.

The ramifications of a host population without

a defined helminth community lends itself to many potential studies. The armadillos on Cumberland Island are unique because this host population coexists on an island with other defined faunal components that may be reservoirs for helminths that could potentially infect them. Certainly, further studies are warranted to determine which of the above hypotheses (the corollary to Brown's theory, or our hypotheses 1, 2, and/or 3), or combination thereof, are valid explanations of why a helminth community failed to establish in an invading host population at the periphery of its native range.

Acknowledgments

We wish to thank Brent Nickol for identification of the larval *M. ingens*. This study was supported in part by Texas Tech University Health Sciences Center, Department of Pathology and by McIntire-Stennis Project GEO-0030-MS-N.

Literature Cited

- Bailey, V. 1905. Biological survey of Texas. United States Department of Agriculture, Bureau of Biological Survey, North America Fauna 25:1-222.
- Bliss, C. I., and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data. *Biometrics* 9:176-200.
- Brown, J. H. 1984. On the relationships between abundance and distribution of species. *American Naturalist* 124:255-279.
- Chandler, A. C. 1946. Helminths of armadillos (*Dasypus novemcinctus*) in eastern Texas. *The Journal of Parasitology* 32:237-241.
- . 1954. The armadillo (*Dasypus novemcinctus*): a review of its natural history, ecology, anatomy and reproductive physiology. Pages 43-66 in R. V. Talmage and G. D. Buchanon, eds. *Rice Institute Pamphlet, Monograph in Biology*. Rice University, Houston, Texas.
- Cleveland, A. G. 1970. The current geographic distribution of the armadillo in the United States. *Texas Journal of Science* 22:90-92.
- Dobson, A. P., and R. M. May. 1984. Patterns of invasion by pathogens and parasites. Pages 58-76 in H. A. Mooney and J. A. Drake, eds. *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York.
- Fedynich, A. M., D. B. Pence, and R. L. Urubek. 1986. Helminth fauna of beaver from central Texas. *Journal of Wildlife Diseases* 22:579-582.
- Galbreath, G. J. 1982. Armadillo *Dasypus novemcinctus*. Pages 71-79 in J. A. Chapman and G. A. Feldhammer, eds. *Wild Mammals of North America: Biology, Management, and Economics*. The Johns Hopkins University Press, Baltimore, Maryland.
- Hillestad, H. O., J. R. Bozeman, A. S. Johnson, C. W. Berisford, and J. I. Richardson. 1975. The ecology of the Cumberland Island National Seashore, Camden County, Georgia. Technical Report Series No. 75-5. Georgia Marine Science Center, University of Georgia, Athens, Georgia. 299 pp.
- Hoberg, E. P., and S. G. McGee. 1982. Helminth parasitism in raccoons, *Procyon lotor hirtus* Nelson and Goldman, in Saskatchewan. *Canadian Journal of Zoology* 60:53-57.
- Humphrey, S. R. 1974. The zoogeography of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. *BioScience* 24:457-462.
- Kisielewska, K. 1970. Ecological organization of intestinal helminth groupings in *Clethrionomys glareolus* (Schreb.) (Rodentia). II. An attempt at an introduction of helminths of *C. glareolus* from the Bialowieza National Park into an island of the Beldany Lake (Mazurian Lakeland). *Acta Parasitologica Polonica* 18:149-162.
- Levine, N. D. 1968. *Nematode Parasites of Domestic Animals and of Man*. Burgess Publishing Co., Minneapolis, Minnesota. 600 pp.
- Margolis, L. G., G. W. Esch, J. C. Holmes, A. M. Kuris, and G. A. Shad. 1982. The use of ecological terms in parasitology (Report of an ad hoc committee of the American Society of Parasitologists). *The Journal of Parasitology* 70:735-746.
- Mayer, J. J. 1989. Occurrence of the nine-banded armadillo, *Dasypus novemcinctus* (Mammalia: Edentata), in South Carolina. *Brimleyana* 15:1-5.
- McBee, K., and R. J. Baker. 1982. *Dasypus novemcinctus*. *Mammalian Species* 162:1-9.
- McNab, B. K. 1980. Energetics and the limits to a temperate distribution in armadillos. *Journal of Mammalogy* 61:606-627.
- Pence, D. B. 1989. Helminth community of mammalian hosts: concepts at the infracommunity, component and compound community levels. Pages 234-260 in G. W. Esch, A. O. Bush, and J. M. Aho, eds. *Parasite communities—Patterns and Process*. Chapman and Hall, London.
- , J. M. Aho, A. O. Bush, A. G. Canaris, J. A. Conti, W. R. Davidson, T. A. Dick, G. W. Esch, T. Goater, W. Fitzpatrick, D. J. Forrester, J. C. Holmes, W. B. Samuel, J. M. Kinsella, J. Moore, R. L. Rausch, W. Threlfall, and T. A. Wheeler. 1988a. Critical comments on a recent letter to the editors regarding the use of frozen carcasses in parasite surveys. *The Journal of Parasitology* 74:197-198.
- , R. J. Warren, and C. R. Ford. 1988b. The helminth community of an insular population of feral swine. *Journal of Wildlife Diseases* 24:105-112.
- Petrochenko, V. I. 1958. *Acanthocephala of Domestic and Wild Animals*. Vol. II. K. I. Skrjabin, ed. Vsesoyuznoe obshchestvo gel'mintologov. Akademiya Nauk SSSR, Moskva. (Translated from Russian [1971] by Israel Program for Scientific Translations Ltd., Keter Press, Jerusalem. 478 pp.)
- SAS Institute, Inc. 1985. *SAS User's Guide: Statistics*. Version 5. SAS Institute, Inc., Cary, North Carolina. 956 pp.

- Taber, F. W.** 1945. Contribution on the life history and ecology of the nine-banded armadillo. *Journal of Mammalogy* 26:211–226.
- Wallace, B. M., and D. B. Pence.** 1986. Population dynamics of the helminth community from migrating blue-winged teal: loss of helminths without replacement on the wintering grounds. *Canadian Journal of Zoology* 64:1765–1773.
- Wobeser, G. A., and T. R. Spraker.** 1980. Post-mortem examination. Pages 89–98 in S. D. Schemnitz, ed. *Wildlife Management Techniques Manual*. The Wildlife Society, Washington, D. C.

MEETING NOTICES

IV International Congress on Malaria and Babesiosis. 13–17 August 1991, Copacabana Palace Hotel, Rio de Janeiro, Brazil. For information write:

Dr. Claudio Tadeu Daniel Ribeiro
Department of Immunology
Oswaldo Cruz Institute, FIOCRUZ
Av. Brasil, 4365
CEP: 21045
Rio de Janeiro, RJ, BRAZIL

XIII International Congress for Tropical Medicine and Malaria. 29 November–4 December 1992, The Ambassador Jomtien Hotel, Choburi, Thailand. For information write:

XIII International Congress for Tropical Medicine
and Malaria
% The Faculty of Tropical Medicine
Mahidol University
420/6 Rajvithi Road
Bangkok, 10400 THAILAND